Allelopathy in the Management of Plant-Parasitic Nematodes[1]

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Abstract: There are numerous reports of nematicidal chemicals in crude plant homogenates, leachates, and decomposing residues. These compounds are usually assumed to be secondary metabolites, which serve as chemical defenses against disease and parasites. When such compounds are released into the rhizosphere, they are known as allelochemicals. The possibility exists to exploit allelochemicals for nematode control, and there have been many attempts to use this approach either by rotation, intercropping, or green manure treatments. Results have met with mixed success. Proof of allelochemical activity in field situations is difficult to obtain, but it is evident that some rotation crops are significantly better at reducing nematode populations than others. Rotations with non-host plants may simply deny the nematode population an adequate food source for reproduction (passive suppression), whereas allelopathic crops kill nematodes by the production of toxic compounds (active suppression). Progress toward sustainable agriculture should benefit from studies on allelopathic nematode control. However, grower acceptance of new plant-rotation strategies are based on economic and logistical considerations as well as efficacy. A potential practical application of allelopathic nematode control that involves using rapeseed as a green manure crop to reduce populations of *Xiphinema americanum sensu lato* in temperate orchards is presented.

Key words: allelopathy, amendment, *Brassica*, glucosinolate, green manure, isothiocyanate, management, nematode, rapeseed, rotation, thioglucosidase, *Xiphinema*.

The term allelopathy was coined in 1937 by Molisch to designate plant-plant and plant-microorganism biochemical interactions. In a review of the subject, Rice stated that Molisch intended the term to include both inhibitory and stimulatory interactions. Rice (30) defined allelopathy as "any direct or indirect, harmful or beneficial effect by one plant (including microorganisms) on another through production of chemical compounds that escape into the environment." Many studies of allelopathy have focused only on interactions in which one organism is detrimentally affected by the association, and only infrequently has reference been made to possible beneficial or stimulatory interactions. In the fifth edition of 'The Dictionary of Scientific and Technical Terms' by McGraw-Hill (2), allelopathy is defined simply as "the harmful effect of one plant or microorganism on another owing to the release of secondary metabolic products into the environment."

Use of the term allelopathy is somewhat controversial. Various disciplines have expanded the meaning to include plant-insect and plant-higher animal biochemical interactions (32,39), and Lovett and Ryuntyu (20) proposed that chemical communications between plants and between plants and other organisms also be considered as examples of allelopathic interaction. Einhellig (11) suggested that allelopathy should be considered an umbrella term to describe all of these interactions, including the chemical defenses of plants. Some authors have proposed that the term "chemical ecology" encompasses all biochemical interactions between organisms and that use of the term allelopathy should be restricted to only plant-plant interactions (27). However, through usage, the broad definition of allelopathy has become widely accepted.

A major principle that separates allelopathy from other types of interactions such as competition is that allelopathy is caused by allelochemicals. Allelochemicals are plant metabolites or their products that are released into the microenvironment. Allelopathic compounds are released through volatilization, exudation from roots, leaching from plants or residues, and decomposition of residues (11,27,39).

Allelopathic interactions have been recognized for centuries, with one of the earliest recorded examples in agriculture dating from 285 BC (28,30). However, it was not until Molisch theorized that biochemical processes might explain these observations that the principles of allelopathy were first established. Only during the past 20 years has there been significant progress in the study of allelopathic chemistry resulting from new techniques which enable the isolation, identification, and quantitative determination of trace natural products in complex matrices such as soil. It was not until such a firm foundation was established that allelopathy became widely recognized as a scientific discipline (27,31, 39).

Allelopathy in Plant Nematology

Plant compounds elicit nematode behaviors such as attraction or repulsion from roots and, therefore, allelopathic research may be considered a fundamental component of nematological research. Because nematodes are recognized as economically important pests, many studies have focused on nematode suppressive crops as potential management tools in cropping systems. Such studies have shown that some crops "actively" reduce nematode populations by the production of nematicidal compounds while others are simply nonhosts (33). The prospect of exploiting naturally occurring allelochemicals for nematode control has advantages over the current use of toxic chemicals, and there have been many attempts to utilize this approach either by rotation, intercropping, or green manure treatments.

The most comprehensively studied example of allelopathy in nematology is that of marigold (*Tagetes* spp.). Marigold has been an important medicinal plant since the first century, and often medicinal plants have been shown to have allelopathic activity (28). Empirical observations indicated that many species of marigold were resistant to a number of nematode species (35,36). Numerous experiments

have since shown that various species and cultivars of marigold can effectively control nematodes on agronomic crops when grown in rotation, interplanted with the crop, or used as a soil amendment (3,29). Also, several nematicidal compounds have been isolated from marigold, with alpha-terthienyl being one of the most potent (17,37,38).

Many crops and weeds have been evaluated for chemical activity against nematodes. Results from these experiments revealed that numerous species, representing many plant families, produce nematicidal compounds. However, the experimental design and sophistication of the techniques used in these studies varied greatly. Only a few studies have provided unequivocal evidence of allelopathy, with most having provided only circumstantial evidence and needing to be substantiated (3,17,28).

Proof of Allelopathy

Many claims of allelopathic activity have been based on results of bioassays using plant homogenates. Merely showing that substances extracted from the roots or leaves of plants cause adverse effects on nematodes in vitro does not provide unequivocal evidence that these compounds are causing allelopathy under natural conditions. Plant homogenates contain various intracellular metabolites, and it seems unlikely that the chemicals extracted from a plant are the same ones normally released into the soil. Such work should not be discouraged, but many plant tissues contain chemicals with potential allelopathic activity and whether these same compounds are released into the rhizosphere in sufficient quantities and with enough persistence to affect nematodes remains a critical question in many cases of alleged allelopathy (8).

There is no specific protocol (similar to Koch's postulates for proof of disease) to establish proof of allelopathy. Nevertheless, to establish a cause-and-effect relationship, the following events must occur in sequence: 1) the allelochemical is pro-

duced, 2) the chemical is transported through the environment from the plant to the target organism, and 3) the target organism is exposed to the chemical in sufficient quantity and for sufficient time to have an effect. Many reports of allelopathic activity have provided evidence for the first and third events, but the critical link between production and exposure has only infrequently been established (7).

Soil is a dynamic and complicated physical, chemical, and biological medium, and organic compounds released into it may be altered and transported by biological and physical means. Cheng (7) broadly classified these processes as retention, transformation, and transport. The retention processes retard the movement of a chemical, the transformation processes change the form or structure of the chemical leading to partial alteration or total decomposition, and the transport processes define how the chemical moves in the soil environment. Each of these processes is complex, and it is beyond the scope of this paper to discuss each in detail. However, the nature of the allelochemical, the microorganisms present, the properties of the soil, and the environmental conditions are key factors that can influence these processes (7,8,11, 27).

The fate of allelochemicals in the environment may vary considerably in different soils and under different conditions, and this may provide an explanation as to why identical (or similar) field experiments have often yielded equivocal results when performed by different workers in different locations. Detailed understanding of allelochemical behavior in soil requires an interdisciplinary approach, and nematologists who study allelopathic interactions would benefit from collaboration with soil scientists, natural product chemists, and rhizosphere biologists.

ALLELOPATHY AND SUSTAINABLE AGRICULTURE

The increasing interest in allelopathy in recent years has resulted in part from a need to develop safer and more ecologically sound pest control strategies. At least two potential benefits may be obtained from allelopathy research. One possibility is the discovery of plant compounds that may lead to new pesticide chemistry having greater efficacy, specificity, and(or) complete decomposition in soil. A second possibility is the identification of efficacious rotation or green manure crops which could be used to control nematodes using conventional or only slightly modified farming practices, thus reducing or eliminating the need to apply nematicides. This latter possibility appears most likely to provide immediate and practical application.

Allelochemicals probably evolved as natural defenses against disease, parasites, herbivores, or encroachment by other plants (15). It has been suggested that plant breeding programs may have unwittingly selected out allelopathic capabilities from crops. Assays to detect allelochemicals appear to support this suggestion. Screening tests have shown a wide range of allelopathic activity in domestic crops. Even among different cultivars of the same crop, some varieties may have substantial allelopathic activity, whereas others apparently have little or none. This situation is analogous to the recognition of genetic resistance in crops to nematodes. When suitable bioassays have been established, it will be possible to select for and breed crops with increased allelopathic activity (16,18).

After decades of high-input farming, agriculture is developing more sustainable practices based on ecologically sound management techniques. These changes involve reduced pesticide use, integrated pest management, greater use of biological controls, and maintenance and improvement of the quality of ground water and soil. Allelopathy appears to be a promising and natural component of sustainable agriculture since the benefits of crop rotation and cover cropping are already well established with regard to maintaining and improving soil quality. However, considerable development is required for the effi-

cient utilization of allelopathic crops in commercial agriculture. Rotations will probably need to be developed specifically for different regions, soil types, nematode problems, and crop production systems. Grower acceptance of allelopathic strategies for controlling nematodes will involve practical considerations such as cost, planting requirements, availability of seed, and efficacy of treatment compared to commercial nematicides.

POTENTIAL OF ALLELOPATHY FOR RENOVATION OF ORCHARD LAND

Various *Brassica* spp. (particularly rapeseed and mustard) have been recognized as beneficial crops for suppression of nematodes, soil-borne diseases, and weeds in crop rotations (6,13,22,24,25,34). Biochemical studies have provided a plausible explanation for the allelopathic activity of this crop. The Brassicaceae are characterized by the production of glucosinolates. These are sulfur-containing glycosides which have a common functional group and a variable side chain (R) that can be aliphatic, aromatic, or heteroaromatic. Upon hydrolysis, glucosinolates produce D-glucose, a sulfate ion, and a range of compounds that can include isothiocyanates, thiocyanates, and nitriles. Some of these byproducts of decomposition can be toxic, and bioassays have shown that they are effective against nematodes (5,9,10,12,14,19,21,23,26,34,40). In laboratory experiments several of these compounds were detected in soil that had been amended with crop residue (1,4,5).

Field and greenhouse experiments in Pennsylvania have shown that rapeseed has potential as a preplant treatment for dagger nematodes (*Xiphinema americanum* Cobb) in replanted orchards when used as green manure (18). In these experiments the greatest decline in the nematode population occurred after incorporation of the crop, and decomposition, presumably, resulted in a release of toxic compounds which either were not present or were present only in sublethal concentrations in the rhizosphere of the growing plant. In the field, a single green manure treatment was not as effective as the nematicide oxamyl, but two successive rotations provided acceptable control.

In Pennsylvania, two rotations are possible within 1 year by planting a winter rapeseed variety in the autumn and again in the spring. The autumn-planted crop will overwinter and resume growth in the spring. The first crop can be turned under in early spring and a second planting made 1 or 2 weeks later. A winter rapeseed variety planted in spring grows vegetatively and does not bolt, thus producing abundant biomass. This second crop can be incorporated in late summer and the site prepared for replanting with fruit trees in the autumn.

Economic considerations are important in commercial agriculture, and since green manure treatments do not provide a crop income and also prevent the growing of alternative crops, it is reasonable to question the acceptance of allelopathy as a nematode management technique by growers. In many cropping systems the use of a green manure rotation may not be justified. However, it appears that this technique may prove acceptable in tree fruit production because it can be incorporated into the existing cropping system.

Old orchard land usually requires extensive renovation in preparation for a new planting. Major steps in the process include removal of old stumps and roots, suppression of plant-parasitic nematodes, adjustments to soil fertility and pH, and management of weeds. In addition, old orchard soil is typically compacted from years of machinery traffic and loss of organic matter where herbicides were used to maintain a vegetation-free zone around trees. One or two years of crop rotation are often used to help remediate these problems since rotations reduce compaction and add organic matter. Tilling the rotation crop provides a window of opportunity to ameliorate fertility and pH problems by incorporation of nutrients and

lime. Also, rotations offer an excellent opportunity to control weed populations with herbicides before the new orchard is established. The ideal rotation crop would also suppress plant-parasitic nematodes and soil-borne diseases by the production of allelochemicals.

The conventional orchard rotation crops in Pennsylvania are typically corn or soybean, which are both good hosts for *Xiphinema americanum*. Thus, while these rotations may help correct some problems associated with replanted orchards, they may also exacerbate the nematode problem and thereby increase the need to fumigate or treat with nematicides. Rapeseed green manure treatments may provide an acceptable alternative for high-value crops such as tree fruit. Although the green manure crop does not provide an income, the savings in fumigation costs can offset the difference.

CONCLUSIONS

The study of allelopathy is now widely recognized as a scientific discipline, and numerous aspects of allelopathy research will have practical application in commercial agriculture to ameliorate pest problems. Nematologists have long recognized the importance of biochemical interactions between plant-parasitic nematodes and their hosts. However, relatively little progress has been made to either understanding the details of these interactions or applying this knowledge toward the development of practical nematode control practices. Much of this can be attributed to a lack of appropriate experimental techniques and a paucity of relevant information regarding natural product chemistry.

Greenhouse and microplot studies have shown that allelopathic rotation crops or green manure treatments can suppress populations of plant-parasitic nematodes, but there are few reports of successful application in commercial agriculture (13,18, 25). In order for allelopathy to be a commercially viable option for nematode control, the technique must be both economical and compatible with farming practices. Despite the apparent potential of this approach, most known allelopathic plants do not fulfill these basic requirements. Common problems encountered include: crops are not adapted to the climate or soil, seeds are too expensive or not available, lack of proper equipment to work the crop, or the benefits of the allelopathic rotation crop are not cost effective compared to nematicide use.

The practical application of allelopathy to control nematodes and(or) other soil-borne diseases need not necessarily depend upon an understanding of the biochemical interaction before it can be implemented. By analogy, many crops have benefited from the deployment of genetic resistance to nematodes without an understanding of how the resistance works. However, suitable bioassays need to be developed for use in screening and evaluating the efficacy of allelopathic crops. Such bioassays are essential for breeding and selecting more effective allelopathic plants.

Allelochemicals in soils are affected by various biotic and abiotic factors. Inconsistencies reported in the efficacy of allelopathy to control nematodes may be attributed to different soil environments or miroflora populations (7). For routine application of allelopathic nematode control in sustainable agriculture, research must be focused toward understanding the conditions required for consistent results. The use of allelopathic rotations will probably need to be adapted to meet the requirements for different cropping systems and nematode problems.

In tree fruit production, a green manure treatment may be cost efficient relative to fumigation or nematicide applications. In addition to suppression of nematodes, a green manure crop can aid renovation of the site by reducing soil compaction, providing organic matter, and helping to control weeds.

Rapeseed appears to be a promising green manure crop for *Xiphinema* sp. nematode control in temperate orchards. The crop is commercially available, inex-

pensive, easily planted, and competitive with weeds. Because rapeseed can be incorporated into a cropping system with little modification of existing practices, growers may be persuaded to try this technique. However, acceptance of this technique as a standard practice will depend upon efficacy and long-term benefits to crop production.

LITERATURE CITED

1. Angus, J. F., P. A. Gardner, J. A. Kirkegaard, and J. M. Desmarchelier. 1994. Biofumigation: Isothiocyanates released from *Brassica* roots inhibit growth of the take-all fungus. Plant and Soil 162: 107–112.

2. Anonymous. 1994. Dictionary of scientific and technical terms. 5th ed. Sybil P. Parker, ed. New York: McGraw-Hill.

3. Bhatti, D. S. 1988. Utilization of toxic plants for the control of nematode pests of economic crops. Final Technical Report. Haryana Agricultural University, Hisar, India.

4. Borek, V., M. J. Morra, P. D. Brown, and J. P. McCaffrey. 1994. Allelochemicals produced during sinigrin decomposition in soil. Journal of Agricultural Food Chemistry 42:1030–1034.

5. Brown, P. D., M. J. Morra, J. P. McCaffrey, D. L. Auld, and L. Williams III. 1991. Allelochemicals produced during glucosinolate degradation in soil. Journal of Chemical Ecology 17:2021–2034.

6. Bullock, D. G. 1992. Crop rotation. Critical reviews in plant sciences 11:309–326.

7. Cheng, H. H. 1992. A conceptual framework for assessing allelochemicals in the soil environment. Pp. 21–29 *in* S. J. H. Rizvi and V. Rizvi, eds. Allelopathy, basic and applied aspects. New York: Chapman and Hall.

8. Cheng, H. H. 1995. Characterization of the mechanisms of allelopathy: Modeling and experimental approaches. Pp. 132–141 *in* K. M. M. Iderjit, Dakshini, and F. A. Einhellig, eds. Allelopathy, organisms, processes, and applications. Washington, DC: American Chemical Society.

9. Chew, F. S. 1988. Biological effects of glucosinolates. Pp. 155–181 *in* H. G. Cutler, ed. Biologically active natural products potential use in agriculture. Washington, DC: American Chemical Society.

10. Duncan, A. J. 1991. Glucosinolates. Pp. 127–147 *in* J. P. D'Mello, C. M. Duffus, and J. H. Duffus, eds. Toxic substances in crop plants. Science Park, Cambridge: Royal Society of Chemistry.

11. Einhellig, F. A. 1995. Allelopathy: Current status and future goals. Pp. 1–24 *in* Inderjit, K. M. M. Dakshini, and F. A. Einhellig, eds. Allelopathy, organisms, processes, and applications. Washington, DC: American Chemical Society.

12. Feeny, P. 1977. Defensive ecology of the cruciferae. Annals of the Missouri Botanical Garden 64: 221–234.

13. Gardner, J., E. P. Casswell-Chen, B. Wester-dahl, C. Anderson, and T. Lanini. 1992. The influence of *Raphanus sativus, Sinapis alba,* and *Phacelia tanacetifolia* on California populations of *Heterodera schachtii.* Journal of Nematology 24:591.

14. Grossman, J. 1993. *Brassica* alternatives to herbicides and soil fumigants. The IPM Practitioner 15: 1–10.

15. Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: To grow or defend. The Quarterly Review of Biology 67:283–335.

16. Inderjit, K. M. M. Dakshini, and Frank A. Einhellig. 1995. Allelopathy: Organisms, processes, and applications. Washington, D.C.: American Chemical Society.

17. Jairajpuri, M. S., M. M. Alam, and I. Ahmad. 1990. Nematode bio-control (aspects and prospects). Delhi, India: CBS Publishers.

18. Jing, G. N. 1994. Evaluation of the nematicidal properties of cruciferous plants for nematode management in replant orchards. Ph.D. dissertation, The Pennsylvania State University, University Park.

19. Lazzeri, L., R. Tacconi, and S. Palmieri. 1993. In vitro activity of some glucosinolates and their reaction products toward a population of the nematode *Heterodera schachtii.* Journal of Agricultural and Food Chemistry 41:825–829.

20. Lovett, J., and Ryuntyu. 1992. Allelopathy: Broadening the context. Pp. 11–17 *in* S. J. H. Rizvi and V. Rizvi, eds. Allelopathy, basic and applied aspects. New York: Chapman and Hall.

21. Mawson, R., R. K. Heaney, M. Piskula, and H. Kozlowska. 1993. Rapeseed meal-glucosinolates and their antinutritional effects. Part 1. Rapeseed production and chemistry of glucosinolates. Die Nahrung 37:131–140.

22. McFadden, W., J. Potter, and J. E. Brandle. 1992. Use of *Brassica* spp. as green manure for biological control of *Pratylenchus penetrans.* Phytopathology 82:246.

23. Mithen, R. 1992. Leaf glucosinolate profiles and their relationship to pest and disease resistance in oilseed rape. Euphytica 63:71–83.

24. Mojtahedi, H., G. S. Santo, A. N. Hang, and J. H. Wilson. 1991. Suppression of root-knot nematode populations with selected rapeseed cultivars as green manure. Journal of Nematology 23:170–174.

25. Mojtahedi, H., G. S. Santo, J. H. Wilson, and A. N. Hang. 1993. Managing *Meloidogyne chitwoodi* on potato with rapeseed as green manure. Plant Disease 77:42–46.

26. Patrick, Z. A., and T. A. Toussoun. 1970. Plant residues and organic amendments in relation to biological control. Pp. 440–459 *in* K. F. Baker and W. C. Snyder, eds. Ecology of soil-borne plant pathogens: Prelude to biological control. Berkeley: University of California Press.

27. Putnam, A. R., and C. Tang. 1986. Allelopathy: State of the science. Pp. 1–19 *in* A. R. Putnam and C. Tang, eds. The science of allelopathy. New York: John Wiley.

28. Rice, E. L. 1983. Pest control with nature's chemicals: Allelochemics and pheromones in gardening and agriculture. Norman: University of Oklahoma Press.

29. Rice, E. L. 1983. Plant-nematode chemical interactions in agriculture. Pp. 50–60 *in* Pest control with nature's chemicals: Allelochemics and pheromones in gardening and agriculture. Norman: University of Oklahoma Press.

30. Rice, E. L. 1984. Allelopathy. 2nd ed., Orlando, FL: Academic Press.

31. Rizvi, S. J. H., H. Haque, V. K. Singh, and V. Rizvi. 1992. A discipline called allelopathy. Pp. 1–10 *in* S. J. H. Rizvi and V. Rizvi, eds. Allelopathy, basic and applied aspects. New York: Chapman and Hall.

32. Rizvi, S. J. H., and V. Rizvi. 1992. Allelopathy, basic and applied aspects. New York: Chapman and Hall.

33. Rodríguez-Kábana, R. 1992. Cropping systems for the management of phytonematodes. Pp. 219–233 *in* F. J. Gommers and P. W. Th. Maas, eds. Nematology from molecule to ecosystem: Proceedings Second International Nematology Congress. Invergowrie, Dundee, Scotland: European Society of Nematologists.

34. Spak, J., L. Kolárová, J. Lewis, and G. R. Fenwick. 1993. The effect of glucosinolates (mustard oil glycosides) and products of their enzymatic degradation on the infectivity of turnip mosaic virus. Biologia Plantarum 35:73–80.

35. Steiner, G. 1941. Nematodes parasitic on and associated with roots of marigold (*Tagetes hybrida*). Proceedings of the Biological Society of Washington 54:31–34.

36. Tyler, J. 1938. Proceedings of the root-knot nematode conference held at Atlanta, Georgia, February 4, 1938. Plant Disease Reporter Supplement 109:133–151.

37. Uhlenbroek, J. H., and J. D. Bijloo. 1958. Investigations on nematicides. I. Isolation and structure of a nematicidal principle occurring in Tagetes roots. Recuceil des Travaux Chimiques des Pays-Bas 77:1004–1008.

38. Uhlenbroek, J. H., and J. D. Bijloo. 1959. Investigations on nematicides. II. Structure of a second nematicidal principle isolated from Tagetes roots. Recuceil des Travaux Chimiques des Pays-Bas 78:382–390.

39. Waller, George R. 1985. Allelochemicals: Role in agriculture and forestry. Washington, DC: American Chemical Society.

40. Williams, L., III, M. J. Morra, P. D. Brown, and J. P. McCaffrey. 1993. Toxicity of allyl isothiocyanate-amended soil to *Limonius californicus* (Mann.) (Coleoptera: Elateriae) wireworms. Journal of Chemical Ecology 19:1033–1046.